

SCANNING ELECTRON MICROSCOPIC STUDIES ON THE
CONTACT CHEMORECEPTORS ON THE PALP-TIP
OF *ORYCTES RHINOCEROS* L. (COLEOPTERA: SCARABAEIDAE)¹

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(With two plates)

Key words: *Oryctes rhinoceros* L., palp-tip sensilla, contact chemoreceptors, blunt-tipped pegs, pointed-tipped pegs, ball-in-socket type pegs, cuticular structures, digitiform sensilla

The terminal segment of the maxillary and labial palpi of *Oryctes rhinoceros* L. has an apical cluster of peg-like sensilla, which bear three morphologically distinct types of pegs, which are described and discussed. Morphology of the digitiform sensillar field, occupying a proximal position on the terminal palpal segment laterally, is also described. The studies concerning the functional modalities of the sensilla are based on the interpretation of structural data obtained via Scanning Electron Microscope analysis.

INTRODUCTION

Studies conducted by the author reveal that the extirpation of the extreme apex of the terminal palpal segments of *Oryctes rhinoceros* L. males renders them incapable of releasing courtship and copulatory behaviour upon contacting the female, whereas contact activation of sexual behaviour was found to be the rule in normal males. Deliberate exploration of the female's body surface employing the palpal tips was found to be a consistent component of the courtship behavioural sequence of the male. Scanning Electron Microscope (SEM) observations of the palpal tips revealed the presence of an apical cluster of peg-like sensilla, surrounded by numerous variously modified cuticular structures and at least some of these palp-tip sensilla are associated with the perception of a certain sexually activating stimulus. The studies also indicate the activating stimulus to be of the nature of a female contact sex pheromone (data to be published). Palpal sensilla, functioning as contact chemoreceptors, have been identified in a number

of insect species (Frings and Frings 1949, Haskell and Mordue 1969, Haskell and Schoonhoven 1969, Klein and Muller 1978, Altner and Prillinger 1980). There are also numerous reports on palpal contact chemoreceptors playing a significant role in feeding behaviour (Blaney and Chapman 1970, Bernays *et al.* 1972, Blaney *et al.* 1973, Mitchell and Schoonhoven 1974), and some reports on their role in host-seeking behaviour (McIver and Charlton 1970). However, though the male palpi making deliberate contacts with the female's body during close-range sexual interactions have been reported in a number of beetles (Selander 1964, Mathieu 1969, Barak and Burkholder 1977), the functional significance of palpal involvement in sexual behaviour is not yet adequately established. Sex recognition via chemosensory filtration through the palpi has been suggested in some blister beetles (Mathieu, 1969). Perception of certain female pheromones via the palpi, facilitating copulation, was speculated for *Attagenus megatoma* Casey (Barak and Burkholder 1977).

The present study is an attempt to infer the probable functions of the palp-tip sensilla of *O. rhinoceros* L. by interpreting the structural data obtained via SEM analysis. The primary

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objective is to corroborate the inference that at least a few of the sensilla on the palpal tips are capable of perceiving a contact chemoreceptive stimulus. This is the first report of its kind on *O. rhinoceros* L., and also provides a morphological base for further electrophysiological studies.

MATERIAL AND METHODS

The maxillary and labial palpi of 35-day-old male and female adults of *O. rhinoceros* L. were analysed, and photomicrographs taken, under a SEM.

RESULTS

The apical cluster of peg-like sensilla on the terminal segment of the maxillary and labial palpi of the male and the female (Plate 1, Figs 1-4) revealed three morphologically different types of sensilla. Of these, the blunt-tipped pegs revealing an apical pore surrounded by movable cuticular processes, and the pointed-tipped pegs disclosing an apical pore on the tip of an eversible papilla, are similar to some of the contact chemoreceptors reported in other insects, while the ball-in-socket type pegs, far less numerous than the other types, are mechanoreceptors, and exhibited prominent sexual dimorphism in arrangement. The peg cluster is surrounded by four basic types of cuticular structures – (1) Open pores of varying sizes representing openings of cuticular glands and/or some cuticle sensillum. Pores bearing (2) a ball-like structure or (3) a dome-shaped spine or (4) a sickle-shaped body. The latter three types are probably mechanoreceptors. Though the shape of the same type of sensilla appeared different under different angles of observation, their apical features provided fairly reliable and easily detectable diagnostic criteria (Plate 1, Fig. 2; Plate 2, Fig. 5). The sensillar types thus recognised were:

1. Ball-in-socket type pegs (BSP) were the most conspicuous and least frequent sensilla, occupying the periphery of the cluster. In the male palpi, they showed a noticeable tendency to congregate towards the upper half of the cluster, which was more obvious in their maxillary palpi (Plate 1, Fig. 1), perhaps due to a greater number of sensilla than in the labial palpi (Plate 1, Fig. 3). In the females, however, the BSP encroached the lower half as well, to varying extents (Plate 1, Fig. 2, 4). Apical phase of the BSP disclosed a cavity bearing a ball-like structure at its centre, presenting a characteristic ball-in-socket appearance (Plate 2, Fig. 7, 8). Between this ball and the rim of the sensillum was a deep groove, of variable width, completely obliterated in some (Plate 1, Fig. 2), whereas others revealed a wide-open groove (Plate 1, Fig. 4). Certain fibre-like processes traversing this groove, between the ball and the rim, were observed in some BSP sensilla (Plate 2, Fig. 7, 8). The number of such connections per sensillum varied from one to four. A small slit splitting the apical rim into a discontinuous ring and forming a dimple-like depression on the side-wall, just below the apex, was another common characteristic (Plate 2, Fig. 7, 8).

(2) Blunt-tipped cylindrical pegs (BTP) had an apical diameter of about 3.13 μm (Plate 2, Fig. 10, 11). A magnification of 10,000x disclosed a slit-like apical pore bordered by a few lobe-like structures in some (Plate 2, Fig. 10) while numerous finger-like processes, apparently closing over an apical pore, were visible in others (Plate 2, Fig. 11).

(3) Pointed-tipped conical pegs (PTP) had an apical diameter of about 0.98 μm . At 10,000x, some of the PTP revealed a simple terminal pore at the tip of an apical papilla. This papilla exhibited a variable morphology ranging from a small protuberance (Plate 2, Fig. 12) to a larger funnel-shaped membranous pouch (Plate 2, Fig. 13). No such papilla was, however, visible in the remaining PTP under the same magnification

(Plate 2, Fig. 16), but a higher magnification of 15,000x revealed a large slit-like aperture at the tip of these 'non-papillate' sensilla (Plate 2, Fig. 17).

The sensilla were arranged in a cluster, with more or less uniform spacing, and the entire cluster was sometimes found as being depressed into the palp-tip (Plate 1, Fig. 2), while it remained everted in others (Plate 1, Fig. 1). The rather circular, and obviously retractile cuticle bearing the cluster revealed an irregular papillate texture, different from the smooth cuticle immediately surrounding it (Plate 1, Fig. 2), and the cuticular surface beyond this smooth area was rough with scaly protuberances (Plate 1, Fig. 3).

The smooth cuticle surrounding the peg-cluster revealed four types of cuticular structures, which were of consistent occurrence, but of inconsistent distribution pattern (Plate 1, Fig. 3). They were (1) Open pores (PO) of varying size, ranging from punctiform pores hardly visible at 600x to those of about 4.2 μm diameter (Plate 2, Fig. 14). (2) Pores bearing a ball-like body at their centre (PB) (Plate 2, Fig. 15). Fibre-like connections extending between this ball and the rim of the pore were observed in some (Plate 1, Fig. 4). (3) Pores bearing sharp-tipped, dome-shaped, spine-like structure (PD) (Plate 1, Fig. 3; Plate 2, Fig. 18). (4) Pores bearing sickle-shaped bodies with pointed or irregular-shaped tip (PS) (Plate 1, Fig. 3; Plate 2, Fig. 19).

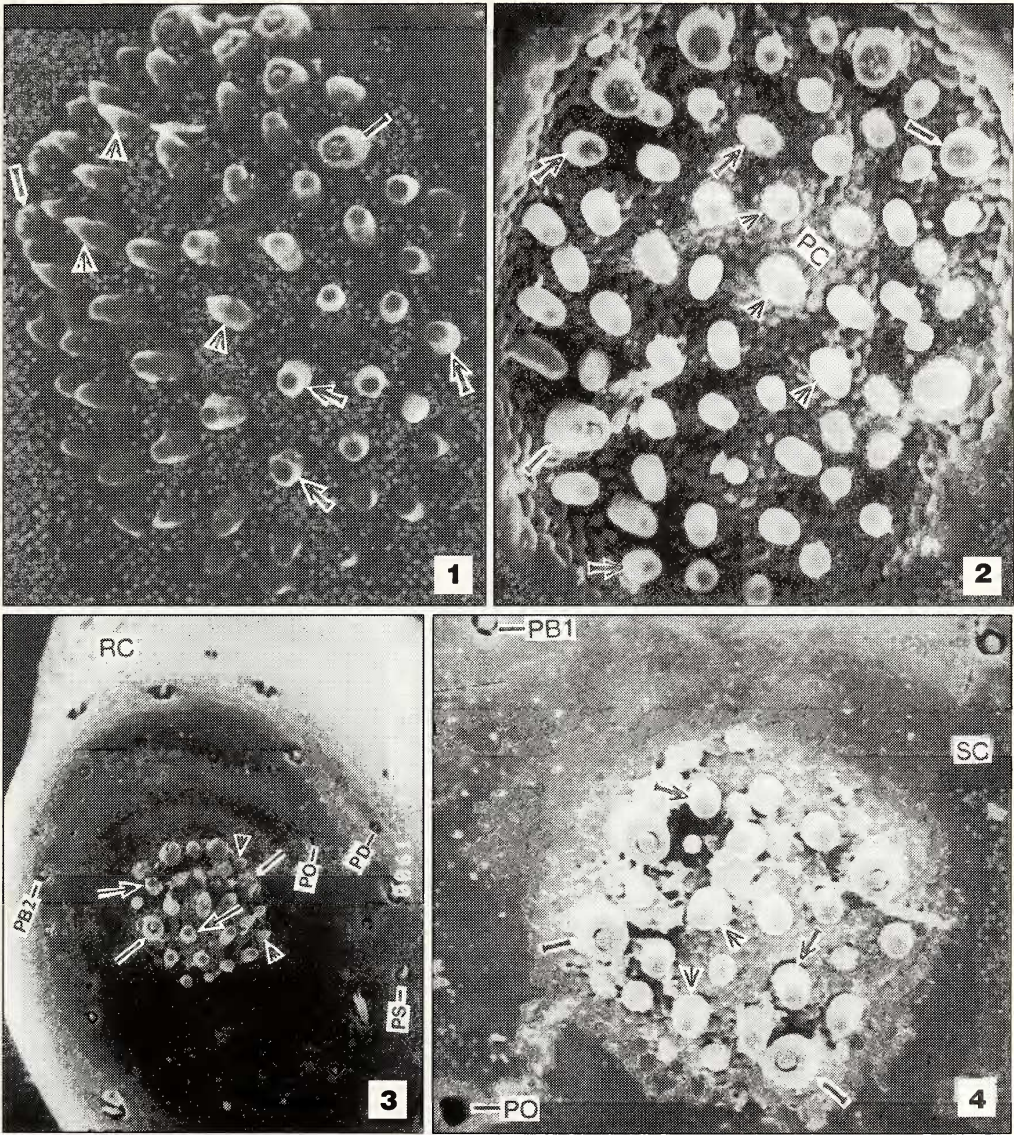
Apart from the apical cluster and surrounding cuticular structures, the terminal palpal segments revealed another prominent sensillar zone, slightly concave and rather oblong, situated latero-dorsally towards its base. It consisted of a dense array of finger-shaped (digitiform) sensilla, each positioned within a correspondingly shaped mesh formed by the surface cuticle (Plate 2, Fig. 6). The proximal end of the mesh was generally slightly tapering, compared to the rather blunt distal end. At 5,000x the sensilla disclosed at their distal end a minute,

subapical protuberance (Plate 2, Fig. 9). The meshy surface cuticle further disclosed a few scattered pores, some of them displaying tubular extrusions, sometimes in the form of tortuous tubes, as being extruded out of, or lying in close association with them (Plate 2, Fig. 6).

DISCUSSION

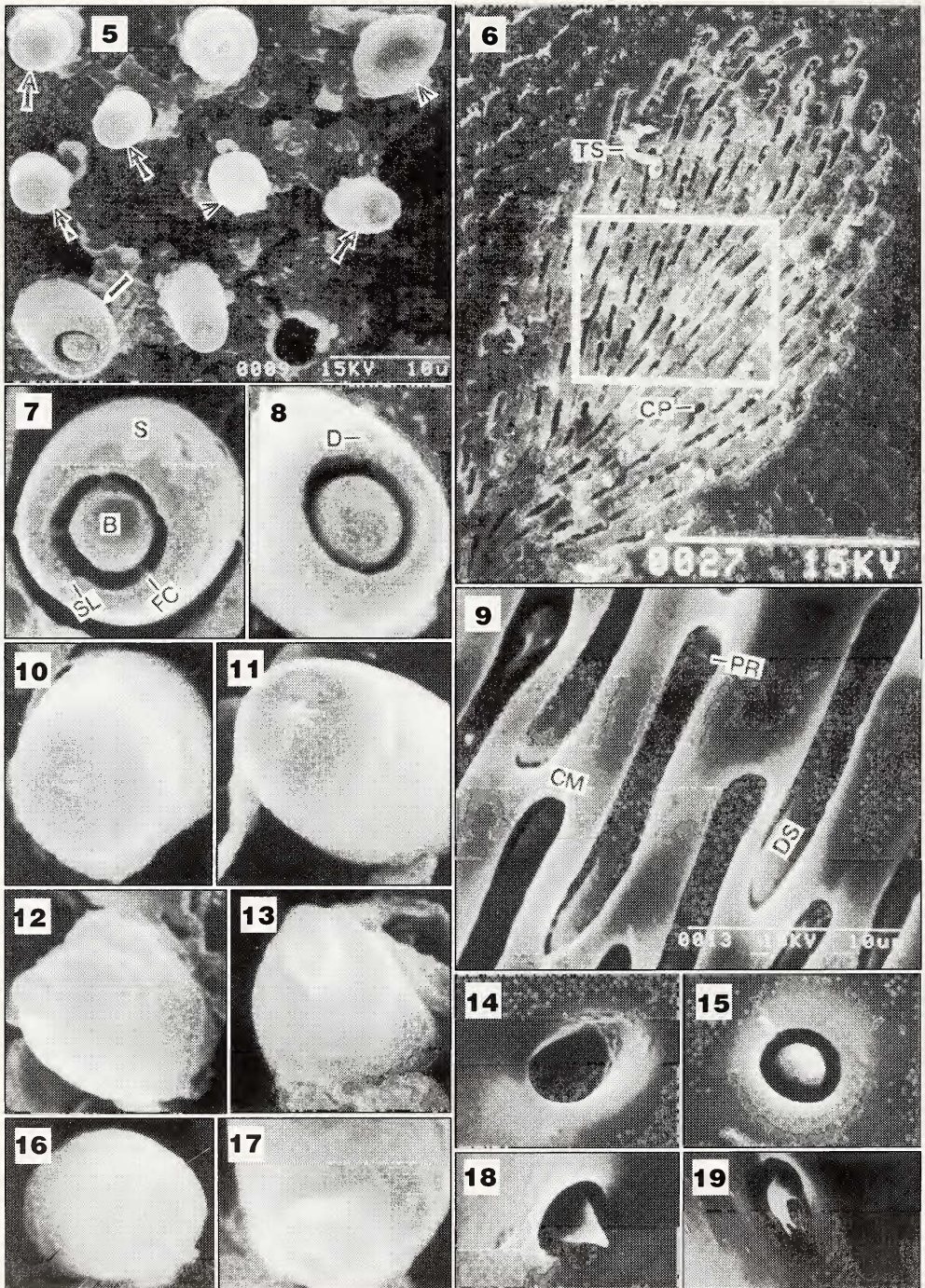
In external morphology, the BSP sensilla are similar to the "mechanosensory nipples" of *Ips typographus* L. (Hallberg 1982) as well as the mechanosensory "Ball-in-tee" companioniform sensilla (Zacharuk 1985). Accordingly, the ball-like structure is the distal end of a central peg positioned within the outer cuticular socket, the former containing within it the sensory element called the tubular body. The above authors do not mention the fibre-like connections radiating between the ball and the socket apically in some of the BSP. Though the number of these connections was found to vary, the presence of four with a more or less symmetrical positioning (Plate 2, Fig. 7) seems to be typical. Whether the absence of such connections in some BSP is due to loss by accident, or reflective of a difference in the physiological state of the sensillum is not clear. That the apical groove of the BSP can remain open or closed to varying extents indicates that these connecting processes are flexible. This suggests their function in the opening and closing of this groove and/or in deflecting the central peg, the latter ability being regarded as a general requisite for mechanoreceptor sensilla (Zacharuk *et al.* 1977, Honomichl and Guse 1981). Like the mechanosensory nipples of *I. typographus* L., the BSP also occupy a peripheral position in the terminal cluster. By correlation of structure and function, a mechanosensory function can be attributed safely to the BSP sensilla.

The significance of sexually dimorphic pattern of distribution of the BSP is uncertain, though it suggests a sex-related difference in their



Figs 1-4: Scanning Electron micrographs of the Palp-tip sensilla of *O. rhinoceros*. The arrows indicate BTP (Blunt-tipped peg), arrow-heads the PTP (Pointed-tipped peg) and the arrow-tails, the BSP (Ball-in-socket peg). 1. Maxillary palp-tip cluster of the male – everted condition (1000x); 2. Maxillary palp-tip cluster of the female – retracted state (1000x); 3. Labial palp-tip cluster of the male with surrounding cuticular structures (600x); 4. Labial palp-tip cluster of the female with a few cuticular structures (1000x).

PB1 – Pore with ball showing fibre-like processes; PB2-Pore with ball showing no fibre-like process, PC-Papillate cuticle; PD-Pore with dome-shaped spine, PO-Open pore, PS-Pore with sickle-shaped body, RC-Rough cuticle.



For caption of Plate 2 see page 369

Plate 2: Figs 5-19: Scanning Electron Micrographs of different sensilla and cuticular structures on the terminal palpal segment of *O. rhinoceros*; 5. Part of a maxillary palp-tip sensillar cluster showing the BTP, PTP and BSP, indicated as in Fig. 1; the large pit represents a shed sensillum (3000x); 6. Digitiform sensillar field of a maxillary palp (600x); 7. BSP showing fibre-like connections (8000x); 8. BSP having no fibre-like connections (8000x); 9. A few digitiform sensilla (5000x); 10. BTP showing lobe-like structures around the apical pore (10,000x); 11. BTP showing finger-like processes presumably closing over the apical pore (10,000x); 12. PTP showing apical papilla as small protuberance bearing the apical pore (10,000x); 13. PTP showing fully everted funnel-shaped apical papilla bearing the apical pore (10,000x); 14. Open Pore (5000x); 15. Pore with ball (5000x); 16. PTP showing no apical papilla (10,000x); 17. "Non-papillate" PTP showing a large aperture apically (15,000x); 18. Pore with dome-shaped spine (5000x); 19. Pore with sickle-shaped body (2000x).

B-Ball, CM-Cuticular mesh, CP-Cuticular pore, D-Depression, DS-Digitiform sensillum; FC-Fibre-like connections; PR-Protuberance; S-Socket; SL-Slit; TS-Tortuous secretion.

function. Perhaps a greater density of these sensilla towards the 'upper' part of the apical phase, as found in the male, may be serving to provide a more intense sensory input during palpation. The significance of the individual variation observed with respect to the number of BSP on the maxillary palpi (6-8) against a fixed number of them in the labial palpi (4) is not known. In *I. typographus* L. the maxillary and labial palpi possess an equal number (2) of mechanosensory nipples (Hallberg 1982).

According to the classification of Snodgrass (1935), the BTP as well as the PTP sensilla are basiconic. As per the typology of Altner (1977), they appear to be uniporous, both revealing an apical pore under the SEM. Presence of a single pore at the tip is a common characteristic of contact chemoreceptive sensilla (Altner 1977, Altner and Prillinger 1980, Zacharuk 1980, 1985). The BTP sensilla with cuticular modifications surrounding the apical pore seem to be uniporous sculptured sensilla (UPS) as described by Zacharuk (1980), and resemble in this respect the electrophysiologically established contact chemoreceptive peg-like sensilla on the palp-tip of Colorado potato beetle larvae (*Leptinotarsa decemlineata* Say) possessing 'villi-like structures' presumably surrounding the sensillar entrance (Mitchell and Schoonhoven 1974) and the contact chemoreceptive uniporous peg sensilla in the antennae of *Tenebrio molitor* L. larvae, which

sometimes revealed 'finger-like projections' surrounding the pore (Bloom *et al.* 1982a). That the cuticular processes of BTP were found to converge apically in some (Plate 2, Fig. 11) while moved apart, appearing as lobes in some others (Plate 2, Fig. 10) suggests that they can open and close. Zacharuk (1980) has pointed out a similar condition in the villi-like processes of the taste receptors of *L. decemlineata* Say (Mitchell and Schoonhoven 1974).

The apical 'molting pore' of aporous sensilla can often be mistaken as the apical pore of uniporous sensilla under the SEM (Zacharuk 1985). Molting pore is the opening through which the dendritic sheath was shed during the previous molt, and is non-permeable (Zacharuk *et al.* 1977, Bloom *et al.* 1982b). Whereas some of the uniporous sensilla showed certain apical sculpturing around the pore, no such modifications are reported in non-permeable molting pores (Zacharuk 1985). The apical molting pore of the blunt-tipped peg sensilla in the antennae of *T. molitor* L. larvae (Bloom *et al.* 1982b) does not show any cuticular modifications, contrary to the apical pore of their uniporous peg sensilla (Bloom *et al.* 1982a). The available data, thus, suggests that the presence of cuticular modifications is implicative of a permeable pore, while their absence may indicate either a permeable pore or a molting pore. Thus, the apical pore of BTP sensilla is most probably a permeable pore, though Transmission Electron

Microscopic studies on its internal ultrastructure are necessary to conclude upon this point.

Terminal papilla as observed in the PTP sensilla of *O. rhinoceros* during the present study are also reported on the basiconic pegs of *Tettigonia viridissima* L. (Henning 1974) and some contact chemoreceptive sensilla of *Apis mellifera* L. (Whitehead and Larsen 1976). In the latter, same kind of sensilla are tipped with either a pore or a papilla, and the papilla is thought to represent either some exudate formed at the tip as reported by Dethier (1972) on the labellar contact chemoreceptor hairs of *Phormia regina* Meigen, or some eversible membrane-like structure. In the present study, the apical papilla of PTP sensilla exhibited an obviously eversible character, as could be evidenced from a series of micrographs depicting different stages of its eversion. The large slit-like aperture seen at the tip of the 'non-papillate' PTP sensilla is seemingly the result of the tucking-in or retraction of the apical papilla. A possible mechanism for the opening and closing of the apical pore is thus envisaged. The terminal pore of the chemoreceptor sensilla on the maxillary palp of *Locusta migratoria* L. is capable of being closed and opened in response to feeding (Bernays *et al.* 1972).

Of the cuticular structures surrounding the peg cluster, the pores bearing ball-like structure (PB) are similar to the 'mechanosensory cuticle sensilla' present on the palpal tips of *I. typographus* L. (Hallberg 1982). As in the BSP, fibre-like connections could be observed radiating between the ball and the rim in some, but not all, of these PB. The striking resemblance between the BSP and the PB in apical morphology is not surprising, in view of a common mechanosensitive function. The pores bearing dome-shaped spine (PD) and those bearing sickle-shaped irregular body (PS) disclosed no visible pores under the SEM. They are most probably mechanoreceptive like the majority of aporous sensilla (Zacharuk 1985).

Functional identity of the open pores (PO), however, is quite uncertain at present. There are three possibilities regarding this: (a) They may be representing certain 'cuticle sensilla' characterised by the absence of any outer cuticular structures, like the single-pore contact chemoreceptors on the maxillary palp-tip of *Agrion puella* and *Ischnura elegans* (Bassemir and Hansen 1980), or the canal sensilla on the tarsal pulvillus of *Schistocerca gregaria* Forskal (White and Chapman 1990). (b) They may be the openings of cuticular glands, perhaps of different types depending on the difference in pore size. Barbier *et al.* (1992) reports similar openings on the terminal segment of maxillary palpi in *Semiadalia undecimnotata* Schn., where the larger openings found among the gustatory receptors on the distal surface are of ductless glands, while the small openings on its lateral sides are of glands with ducts. Such openings are also present over the entire body and appendages of adult males and females. In *O. rhinoceros* L. also the PO like structures are of wider distribution, as could be detected on the cephalic capsule, prothorax, pygidium and elytra of both sexes (author's unpublished data). (c) Some of the PO may be representing cuticle sensilla, and others, the gland openings.

Digitiform sensillar fields comparable to those in *O. rhinoceros* L. are present in a corresponding position in adult *Dermestes maculatus* De Geer (Honomichl and Guse 1981), *I. typographus* L. (Hallberg 1982) and *Ctenicera destructor* Brown (Zacharuk *et al.* 1977). In *T. molitor* L., adult digitiform sensilla are distributed in a scattered fashion (Honomichl and Guse 1981). In *O. rhinoceros* L., digitiform sensillar field occur on both the maxillary and labial palpi, as also in *Dendroctonus ponderosae* Hopkins (Whitehead 1981) but in *I. typographus* L. they are lacking in the labial palpi (Hallberg 1982).

The cuticular pores scattered over the digitiform sensillar field of *O. rhinoceros* L.

apparently correspond to the dermal gland openings occurring in association with the digitiform sensilla of *Dermestes* (Honomichl and Guse 1981). Presence of associated tubular extrusions appropriating with the pore diameter provides solid evidence for the glandular function of these pores in *O. rhinoceros* L. In *S. undecimnotata* Schn. also, a similar tortuous cylinder escaping out of the labellar gland opening was visualised under the SEM (Barbier *et al.* 1992). Digitiform sensilla of *C. destructor* Brown reveal a molting pore near their tip at 12,000x magnification (Zacharuk *et al.* 1977). The sub-apical protuberance appearing invariably in all the observed digitiform sensilla of *O. rhinoceros* L. at 5,000x might be representing a molting pore.

In spite of superficial homologies, there can be considerable difference in internal ultrastructure between the digitiform sensilla of different species, e.g., between those of *Dermestes maculatus* De Geer (Honomichl and Guse 1981) and *C. destructor* Brown (Zacharuk *et al.* 1977), which were considered as thermoreceptors and mechanoreceptors respectively. The present data

is not sufficient to derive the function of the sensilla in *Oryctes rhinoceros* L.

The present studies provide morphological evidence for the presence of two types of contact chemoreceptors, comprising a major portion of the palp-tip cluster, of which at least one is presumably associated with the perception of aphrodisiac contact sex pheromone. Further TEM as well as electro-physiological studies may serve to confirm the present findings.

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